

Aspects of the Microbial Ecology of Forest Ecosystems

Dennis Parkinson

INTRODUCTION

Since the 1950's there have been regular and, at times, detailed studies of the microbial ecology of forest soils in which most detailed attention was given to microorganisms in the organic horizon. In the initial studies a great deal of attention was paid to the microorganisms isolated from the different layers of the organic horizon. The fungi were, and in fact still are, the group of microorganisms most studied, and attempts have been made to elucidate "successional patterns" of these organisms and their roles in decomposing leaf litter on the forest floor (Hayes, 1979).

Subsequently, interest became more directed to the general phenomenon of organic matter decomposition in forest soils. Through detailed studies, mainly using litter bag methods, information was gathered on rates of organic matter decomposition on a range of sites. From such studies a number of generalizations have been postulated (and have become part of the lore of decomposition!). Quality of the substrate(s) undergoing decomposition has been shown to be a major factor governing decomposition rates; there being a negative correlation of such rates with initial lignin content and C:N of the substrates, and a positive correlation with soluble carbohydrate and (to a lesser extent) N and P contents. Climatic factors of temperature and moisture were found to be important governing factors. Thus, in dry exposed sites decomposition rates were severely restricted in standing dead material, but tended to increase within the soil profile. Whereas in wet climates, decomposition rates of standing dead and surface litter were high but might decline with profile depth. Of course, freeze-thaw and drying-re-wetting events over short periods of

time play a very important role in nutrient release from decomposing leaf litter. In general, there is an increase in decomposition rates in the temperature "transect" from pole to equator. Finally, the availability of suitable decomposer organisms is essential. It is well known that following an initial weathering period, during which time leaching of soluble nutrients from freshly fallen litter occurs, the decomposition process is effected by microorganisms and litter and soil invertebrates. Therefore, interest has been re-directed to the roles of decomposer organisms in litter decomposition and consequent nutrient cycling.

Whilst the range of interactions between invertebrate fauna and microflora has been known for a considerable period of time, only relatively recently have detailed studies been made in attempt to quantify these interactions and to assess their possible consequences in the cycling of nutrients in forest ecosystems.

In this presentation attention will be centered on two aspects of forest microbial ecology that have received considerable attention over the past few years. Firstly, to microbial biomass determinations in decomposing litter on the forest floor. This may appear to be a "perennial topic"; however, new methods of obtaining reliable data are being developed to allow better quantitative assessment of nutrient tie-up (and release) in the microorganisms. Secondly, some comments will be made on recent work on specific fungus-fauna interactions which may affect the pattern of fungal colonization and decomposition of organic matter.

A considerable body of excellent publications is available in both these areas, but this presentation will deal specifically with two case studies involving the author. References to the research will be minimized.

STUDIES ON MICROBIAL BIOMASS
OF FOREST LITTER LAYERS

One of the factors impeding the development of studies on the participation of microorganisms in forest ecosystems has been the lack of suitable methods for rapidly assessing total microbial biomass in soils and organic matter, fluctuations of that biomass, and the relative contributions of fungi and bacteria to this biomass. Direct observation methods have been used in several studies of fungi in leaf litter decomposing on the forest floor, but the techniques used (Frankland, 1975; Visser and Parkinson, 1975) are time consuming and probably underestimate total lengths of fungal hyphae associated with the leaf debris. Furthermore, in many cases, it is difficult to distinguish live hyphae from dead. The use of phase-contrast microscopy partly overcomes the difficulty of distinguishing hyphae with cell contents from empty hyphae. Using this method, Frankland (1975) calculated that of the 289 μg fungi g^{-1} L layer litter (deciduous woodland) about 35 percent was "live" (possessed cell contents), whilst Visser and Parkinson (1975) calculated that the fungal standing crop of L layer leaves in a *Populus tremuloides* woodland at the time of snowmelt was about 1,421 mg dwt m^{-2} with more than 50 percent of observed hyphae containing protoplasm.

These data can be compared with those for live hyphal data obtained for oak-beech forest L and F layer litter of 79 to 82 percent and 15 to 20 percent respectively (Nagel de Boois and Jansen, 1971), and 76 to 97 percent of observed mycelium being active during initial stages of decomposition of beech leaves (Waid, Preston, and Harris, 1973). However, Soderstrom (1979), using fluorescent staining (fluorescein diacetate), has recorded much lower values for "live" hyphae in soil (2-3%).

Direct observation methods, being time consuming in operation, are difficult to apply in large comparative studies on fungal biomass changes that require very frequent sampling (replicate). Chemical techniques have been developed for specific studies (e.g., chitin determination, Swift, 1973) or for general investigations (ATP determinations). Recently Anderson and Domsch (1978) described a rapid method for total microbial biomass determinations in soil samples, and when this method is coupled with the selective inhibition method (Anderson and Domsch, 1975) determinations of bacterial and fungal biomass are possible. While this total method was originally developed for studies on agricultural soils, it has been valuable for detailed investi-

gations of the organic horizon of forest soils (Parkinson et al., 1978).

This method was used in a detailed study of three spruce (*Picea abies*) soils in the Solling area of Germany, but only one site (a 95-year-old spruce site) will be discussed here. Firstly, tests showed that measurements on composite organic horizon samples could give an accurate index of the microbial biomass in the organic horizon (L, F, and H layers). Then the Anderson and Domsch (1978) method was used on regularly taken samples (at least once per month over 10 months) from the field, and the effects of moisture content and temperature of the organic horizon were investigated under laboratory conditions. From these studies the following major points emerged:

1. Maximum total microbial biomass developed at about 15°C and in the 60 to 80 percent moisture range. These data allowed simple predictions for the spruce forest site which were testable against actual determinations on field samples. March samples were taken at field conditions where the temperature of the organic layer was + 1.5°C with 65 percent moisture, and from these data the predicted total microbial biomass was 180.0 to 190.0 mg C 100 gdw^{-1} . In May the organic horizon temperature and moisture conditions were + 14.0°C and 65 percent, the predicted microbial biomass was 320.0 to 330.0 mg C 100 gdw^{-1} , and the observed value was $304.0 \pm 8.4 \text{ mg C 100 gdw}^{-1}$.

2. Seasonal microbial biomass changes ranged between 194 mg C 100 gdw^{-1} (late autumn-winter) and 310 mg C 100 gdw^{-1} (late spring-summer). However, particularly in autumn and spring when more marked diurnal variations in temperature would be expected, considerable microbial biomass variations would be expected and in fact were observed. In autumn, between 6 and 20 September total microbial biomass increased by 48 percent, whereas in the next 10 days (20-30 Sept.) it fell by 7 percent and by late October it had fallen by a further 32 percent. In the spring, between 9-17 March there was a 43 percent increase in microbial biomass which was followed (17 March - 4 April) by a 27 percent fall. These periods would be expected to be ones of a drastic changes in nutrient tie-up and release. Gross calculations of C "tie-up" and release during the year (not taking into account any "internal recycling" of C within the decomposer complex) would indicate an overall release of 105 mg C 100 gdw^{-1} organic horizon between 20 September and 9 March; while, between 9 March and 6 June there was a C tie-up of 116 mg C 100 gdw^{-1} .

3. Considering the annual mean temperature (and the absence of limiting moisture conditions at the experimental site during the study period), an annual mean microbial biomass of about 212 mg C 100 gdw⁻¹ (or about 9.6 g microbial C m⁻²) could be expected. Selective inhibition experiments indicated the average partitioning of the total microbial biomass was 77 percent fungi and 23 percent bacteria.

4. In view of the comments made regarding the calculation of bacterial maintenance requirements and substrate available for microbial growth in forest soils (Gray and Williams, 1971; Hissett and Gray, 1976), an attempt was made to assess the implications of the annual microbial biomass in the organic horizon of the spruce forest. The following summary carbon balance sheet could be made up:

Input of above	
ground litter :	230 g C m ⁻² yr ⁻¹
Estimated input of	
root exudates	
and dead roots :	70 g C m ⁻² yr ⁻¹
Output of leachates	
from the H layer	
(data from Ulrich,	
pers. comm.) :	34 g C m ⁻² yr ⁻¹

i.e., in a 'steady state' condition (no accumulation, no depletion) 266 g C m⁻² yr⁻¹ would be available for microbial maintenance and growth.

However, in the 95-year-old spruce forest studied it was more reasonable to assume that some organic matter accumulation was still occurring. In comparing weights per square meter of organic horizons of spruce forests of different ages in the Solling area it was estimated that accumulation at the study site could be occurring at the rate of 20 g C m⁻² yr⁻¹.

Therefore, 246 g C m⁻² yr⁻¹ would actually be available for microbial maintenance and development.

Data from selective inhibition studies indicated that the average yearly total microbial biomass of 9.6 g C m⁻² was made up of 2.2 g bacterial C and 7.4 g fungal C. Assuming a yield coefficient of 0.5 and a maintenance constant of 0.001 hr⁻¹ (Hissett and Gray, 1976), then: 56.6 g C m⁻² yr⁻¹ would be available for bacterial maintenance and turnover, of which 38.5 g C m⁻² yr⁻¹ would be required for maintenance, leaving 18.1 g C m⁻² yr⁻¹ available for 'turnover' (which would allow a mean generation time of about 45 days). 189.4 g C m⁻² yr⁻¹ would be available for fungal maintenance and growth.

Undoubtedly these calculations are primitive, as they do not take any account

of the recycling of microbial carbon within the complex decomposer system. However, they do indicate the availability of resources to support the level of microbial biomass recorded.

The method of Anderson and Domsch (1978) was also applied to a study of three spruce forests of different ages (Parkinson et al., in press). In this study an attempt was made to assess direct relationships between primary production parameters and decomposer biomass and respiratory activity. Fortunately, a considerable body of data on the primary producers was available since the three chosen spruce sites were studied in the German IBP (many of these data were published by Ulrich et al., 1974, and unpublished data were provided by Dr. Heller).

The ages of the three study sites were 48, 95, and 123 years. The highest above-ground standing crop was seen in the 95-year-old site and the lowest value was at the oldest site. Aboveground productivity was highest at the youngest site; the lowest value was recorded at the oldest site.

Estimation of annual productivity per unit weight of standing crop (based on unpublished data, Heller, pers. comm.) yielded the somewhat curious data given in Table 1, with the middle-aged site showing the lowest value. Table 1 also presents similar data based on estimations of standing crop and productivity made in 1968 (Ulrich et al., 1974).

The total standing crop of roots in the organic horizon was significantly higher at the youngest site, and the proportion of mycorrhizal roots was also highest at this site.

Data on the organic horizon at each study site are given in Table 1. These indicate that the contribution of L + F₁ layers to the total organic horizon varied considerably from site to site (highest in the youngest site, lowest in the oldest). They also indicate variations from site to site in percent C, percent N and C/N. From the data on total weight of organic matter (m⁻²) of the organic horizon at each site, it would appear that the weight of the organic horizon (m⁻²) at the middle-aged site (95 years), i.e., 4,545 g m⁻² was much less than would be expected. Given the age of the site plus the data obtained from the other sites, 9,000 to 10,000 gdw⁻¹ litter m⁻² would be expected for this site.

The data on basal respiration of the total organic horizon material (measured at 22°C) are given in Table 2. However, the mean annual temperature for all sites was 6.2°C. Laboratory experiments at this mean annual temperature indicated that the loss of carbon m⁻² yr⁻¹ at each site would be

Table 1. General data on primary producers and allied material for each of the study sites.

Site age	48 years	95 years	123 years
Aboveground standing crop 1968 (g m^{-2})	14,300	24,446	23,500
Aboveground standing crop 1977 (g m^{-2})	17,741	26,884	15,823
Aboveground productivity 1968 ($\text{g m}^{-2} \text{ yr}^{-1}$)	849	886	651
Aboveground productivity 1977 ($\text{g m}^{-2} \text{ yr}^{-1}$)	767	525	441
<u>Productivity</u> Standing crop 1968	0.059	0.036	0.029
<u>Productivity</u> Standing crop 1977	0.043	0.0195	0.028
Total weight (g m^{-2}) organic horizon	5,207	4,545	11,453
Percent contribution of L + F ₁ to organic horizon	10.3	7.3	5.8
Percent organic matter in organic horizon (composite)	83.6	75.8	69.3
Percent C	42.5	39.2	36.6
Percent N	1.6	1.4	1.3
Roots (<5 mm diam.) standing crop (g m^{-2}) in organic horizon	216	78	146
Mycorrhizal roots (g m^{-2})	97	10	43

Table 2. Average yearly basal respiration of composite organic horizon samples from the three study sites (measurements made at 22°C)

	Average yearly value	
	$\text{ml CO}_2 \uparrow 100 \text{ g dwt}^{-1} \text{ hr}^{-1}$	$\text{g C} \uparrow \text{m}^{-2} \text{ hr}^{-1}$
48-year-old site	3.47	0.097
95-year-old site	1.80	0.044
123-year-old site	1.36	0.084

approximately: 48-year-old site: $266 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95-year-old site: $114 \text{ g C m}^{-2} \text{ yr}^{-1}$; 123-year-old site: $206 \text{ g C m}^{-2} \text{ yr}^{-1}$.

General data on total microbial biomass at each of the three study sites are given in Table 3. Selective inhibition experiments indicated no significant variations in the percentage contribution of bacteria and fungi to this total biomass over the 10-month study (the ratio bacteria: fungi remaining constant at 20:80). The data indicate that, on the basis of 100 gdw organic horizon samples, average total microbial biomass was highest in the youngest site and lowest at the oldest site. When calculated on a square-meter basis this order was altered, the youngest site still holding the highest microbial biomass but the middle-aged site holding the lowest. Similar relationships were observed when considering data on maximum microbial biomass change at each site over the study period -- a parameter which is at best crude because of the demonstrated short-term large fluctuations in total microbial biomass in coniferous forest organic horizons (Parkinson et al., 1978).

By any form of calculation, the organic horizon of the youngest site emerged as having both the highest activity (as indicated by basal respiration measurements in Table 2) and the highest microbial biomass (Table 3). Furthermore the variations (both positive and negative) in total microbial biomass during the study period (Nov. - July) were much greater at this site than at the other two sites. Since the important environmental factors of temperature and moisture content of the organic horizon at each site were essentially similar, other reasons must be sought for the higher microbial activity and biomass (plus fluctuations) at the youngest site.

Judging by the data in Table 1, the major differences between the three study sites were:

1. There was a higher contribution of L + F₁ layer material to the total organic horizon (10.3% at the youngest site, 7.3% at the middle-aged site, and 5.8% at the oldest site). In a detailed study of the 95-year-old site, Parkinson et al. showed the L + F₁ layer material to be the locus of highest biological activity and microbial biomass. Therefore, this greater contribution at the youngest site is probably an important phenomenon in allowing the high values.

2. The percentage carbon in the organic layer was highest at the youngest site, and the C/N was narrowest.

3. There was a higher standing crop of roots in the organic horizon of the youngest site. There were also considerably more mycorrhizal rootlets in the F₂ and H layers of the youngest site than in the other sites.

Presumably this larger root standing crop would, via exudates and sloughed-off material plus input of dead roots, enhance microbial activity and development. A proportion of the microbial biomass determined, at least in the spring and summer samples, could be mycorrhizal fungal material (hyphae growing into the organic horizon from mycorrhizal sheaths).

These factors at the youngest site are enhanced by the figures given in Table 1 on primary productivity per unit aboveground standing crop, where the youngest site gave the highest values both in 1968 and 1977 (0.059 and 0.043).

The oldest site which, on the basis of unit weight (100 gdw) of organic horizon, had the lowest basal respiration and total microbial biomass values, was also the site with the highest amounts of F₂ and H layer

Table 3. Summary of total microbial biomass values in composite organic horizon samples from the three study sites.

	Average yearly total microbial biomass values		Maximum - minimum biomass values	
	mg C 100 gdw ⁻¹	g C m ⁻²	mg C 100 gdw ⁻¹	g C m ⁻²
48-year-old site	571.9	29.8	342.7	17.9
95-year-old site	260.0	11.8	116.4	5.3
123-year-old site	209.7	24.0	84.6	9.7

Table 4. Summary of microbial and primary producer (and allied) data on a comparative, proportional basis

	Microbial (decomposer) parameters			Primary producer (and allied) parameters		
	Basal respiration	Average total biomass	Max-min biomass	Productivity standing crop	Roots <5 mm	Percent contribution of L + F ₁
1. m ⁻²						
48-year-old site	2.2	2.53	3.38	2.2	2.77	1.78
95-year-old site	1.0	1.0	1.0	1.0	1.0	1.23
123-year-old site	1.9	2.03	1.8	1.4	1.87	1.0
2. 100 gdw ⁻¹						
48-year-old site	2.55	2.72	4.05	2.2	3.26	1.78
95-year-old site	1.32	1.24	1.38	1.0	1.35	1.23
123-year-old site	1.0	1.0	1.0	1.4	1.0	1.0

material per sample (and, naturally, per m^2). The total amount of roots at this site was not significantly different from that found at the middle-aged site, but higher amounts of mycorrhizal roots were present as compared with the middle-aged site. Data on aboveground productivity per unit standing crop (Table 1) at the oldest site changed only very slightly in the 1968-1977 period (0.0288 in 1968 and 0.0278 in 1977). However, similar data for the middle-aged site (Table 1) indicated a considerable decline in primary productivity per unit standing crop of primary producers during the same period (0.036 in 1968 and 0.0195 in 1977).

When calculating microbial biomass on a square-meter basis for each site, it is impossible to deal with the paradox of the low total weight (m^{-2}) of the organic horizon at the middle-aged site. However, weights (m^{-2}) of the organic horizon at each study site compared with similar measurements obtained in 1968 (Ulrich et al., 1974) as follows:

	Site A	Site B	Site C
1968 data (Ulrich et al., 1974)	5,200 g m^{-2}	4,900 g m^{-2}	11,100 g m^{-2}
1976-1977 data (Parkinson et al., in press)	5,207 g m^{-2}	4,545 g m^{-2}	11,453 g m^{-2}

No significant change in the mass of organic horizon has occurred over almost a decade. Does this mean there is a steady state condition in this horizon at each site?

Table 4 summarizes the comparative (proportional) relationships of several microbial (decomposer) parameters and primary producer (and allied) parameters for each site. The data are given both for unit weights (100 gdw) of organic horizon and on a square-meter basis. These data reinforce the comments made earlier on the three study sites. It is well known that chemical quality of litter substrates and input of material from roots (live and dead) are important factors in affecting decomposer biomass and activity in any soil, and the data exemplify this fact for the three study sites. However, relationships between primary productive vigour (productivity/standing crop) and decomposer activity and biomass (per m^2) are also indicated. While the proportional relationships of basal respiratory activity and primary productivity per unit standing crop for the three sites are very similar, other relationships are not as direct as might have been expected. The situation, particularly at the middle-aged site, has been complicated by a complex history of the vegetation (probably prior to 1968). The data provided here indicate the type of parameters which should be considered in attempting to derive re-

lationships of primary producers and decomposers, and further indicate the power of the physiological method (Anderson and Domsch, 1978) for microbial biomass determinations.

The previous comments indicate some interesting approaches, given a speedy method for microbial biomass assessment. The data can be further extended to consideration of nutrient cycling if knowledge of the other nutrients held in microbial tissue is considered (Visser and Parkinson, 1975). Regrettably, too little is known on actual microbial turnover rates in forest soils, the actual ecological efficiency of the important soil bacteria and fungi, and on death and decay rates of the various components of the litter and soil microbiota.

INTERACTION BETWEEN MICROFLORA AND FAUNA IN FOREST LITTER

Efficient organic matter decomposition in the surface layers of forest soils is effected by the joint activities of the microflora and the soil fauna. Bacteria and fungi are generally considered to play by far the major role in the actual oxidation of organic carbon, although it has been demonstrated that some of the soil animals can act as agents of primary decomposition because they possess cellulolytic enzymes in their guts. Nevertheless, the major roles in organic matter decomposition attributed to the soil fauna are:

1. Transmission of microbial inoculum in organic matter.
2. Fragmentation of large pieces of organic matter, with the consequent increase in surface area exposed for microbial development.
3. Possible enhancement of microbial activity because of changes in the chemical constitution of organic material during passage through the animal gut.
4. Possible effects (stimulatory or inhibitory) on the microflora as a result of animal grazing on that microflora.

Among the fauna active in the organic layers of the forest floor are various groups which, at least during part of their life history, consume microbial tissue. A

good deal of attention has been directed to the consumption of fungi by microarthropods, and when attempts have been made to assess the actual amounts of consumption of fungi by various groups of these microarthropods in field locations, the values obtained have been frequently low. Various taxa of the microarthropods that graze on fungi do not consume all species of fungi -- they selectively consume specific groups of the mycoflora in decomposing litter. The possible implications of this selective grazing will be discussed later.

Active consumption of microbial tissue by microarthropods could restrict nutrient loss (via leaching) from decomposing organic matter. Further indication of role of soil animals as stabilizers of nutrient cycling comes from the evidence that these organisms concentrate certain nutrient elements (K and Ca) in their tissues. Also the faeces of some microarthropods (particularly mites) are slowly decomposed and thus nutrients held in the faeces are only slowly released (elemental leaching is retarded).

In a cool, temperate, deciduous forest dominated by Populus tremuloides (Lousier and Parkinson, 1976, 1978 have given general decomposition and nutrient dynamics of this area), Mitchell (1976) calculated that consumption of fungi by Oribatid mites was $6 \text{ g m}^{-2} \text{ yr}^{-1}$, a figure which represented about 2 percent of the fungal standing crop. In this particular forest, Visser and Parkinson (1975) observed a high fungal standing crop ($1,421 \text{ mg dwt m}^{-2}$) in the litter layer at the time of snowmelt (April), and that this standing crop rapidly declined (to $786 \text{ mg dwt m}^{-2}$) immediately following snowmelt. This quantitative change in fungal standing crop was accompanied by a significant qualitative change in the fungal community in the L layer litter. Before snowmelt, Basidiomycetes were isolated with a frequency of about 3 percent, and after snowmelt their frequency of occurrence was about 14 percent. Before snowmelt, sterile dark hyphal forms were isolated with about 26 percent frequency, but this fell to 14 percent after snowmelt. At the same time, Collembola were observed to be numerous and active in the litter layer, suggesting that high grazing activity by these animals could be one factor responsible for this decline in fungal standing crop.

A detailed study showed that one species of the Collembola (Onychiurus subtenuis) was particularly frequent in the surface organic matter during the snowmelt period (about 4,500 animals m^{-2} in the L layer). Examination of gut contents and of faeces indicated this species was selectively grazing on fungi possessing dark

hyphae. A food preference study (Visser and Whittaker, 1977) confirmed that selective feeding by O. subtenuis on sterile dark fungi did, in fact, occur.

Following this, the effect of grazing by O. subtenuis on the two commonly recorded, potentially competitive, groups of litter fungi (Basidiomycetes and sterile dark forms) was investigated. A single common Basidiomycete species and a single common sterile dark form, which possessed similar growth rates when grown on L layer leaf litter, were chosen for study. The microcosm experiments have been described in detail (Parkinson et al., 1977; in press), so only the general conclusions will be outlined here. The selective grazing by the Collembola could have significant effects both on fungal growth in the L layer leaf litter surfaces, and on the colonization by fungi of dead leaf material on the litter surface. In essence, the selective grazing by the animals on the sterile dark fungus tilted the balance of competition in favor of the Basidiomycete. An interesting additional fact is that the Basidiomycete used in these experiments was apparently toxic to the test animals. The Basidiomycete was capable of actively utilizing cellulose whereas the sterile dark form was not, hence the selective grazing of the animals could have very marked effects on the rate and course of litter decomposition.

Thus grazing by invertebrates on fungi in forest litter is probably a much more complex phenomenon than would appear from quantitative studies on ingestion, i.e., relatively low grazing levels could have magnified effects, if selective, by reinforcing or switching competitive relationships between litter fungi.

When Collembola are allowed to move freely in microcosms containing sterile leaves or coarse sterile macerate for 5 to 10 days, it is found that when pieces of the sterile substrate are plated many of them yield bacteria and/or fungi. With respect to O. subtenuis, very few fecal pellets of this animal yielded fungi when plated onto 2 percent malt agar (only 2 of 40 plated pellets yield fungi -- in this case, a Mortierella -- even though they contained fungal hyphae). Thus it appears that the animals carry microbial "inoculum" on their external surfaces and are efficient spreaders of inoculum within organic matter. Apart from this being an interesting and potentially important phenomenon in nature, it does cause problems in studying, by respirometric methods, the positive or negative effects of animal grazing on fungal growth and activity in decomposing litter -- it has been suggested that grazing removes senescent hyphae and stimulates fungal growth.

This contribution has dealt with only two aspects of the microbiology of forest organic matter. Topics such as wood decomposition, mycorrhizal associations and the biology of mycorrhizal fungi, nitrogen transformations and a range of intermicrobe interactions are currently under detailed study. These studies will provide clearer ideas on the detailed functions of decomposer organisms in forest ecosystems.

LITERATURE CITED

- Anderson, J. P. E., and K. H. Domsch. 1975. Measurement of bacterial and fungal contributions to respiration of selected agricultural and forest soils. *Can. J. Microbiol.* 21:314-322.
- Anderson, J. P. E., and K. H. Domsch. 1978. A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biol. Biochem.* 10:215-221.
- Frankland, J. C. 1975. Fungal decomposition of leaf litter in a deciduous woodland. In Biodegradation et Humification, edited by G. Kilbertus et al. pp. 33-44. Sarreguemines, France: Pierron Editeur.
- Gray, T. R. G., and S. T. Williams. 1971. Microbial productivity in soil. In Microbes and Biological Productivity. Symp. Soc. Gen. Microbiol. 21:255-286.
- Hayes, A. J. 1979. The microbiology of plant litter decomposition. *Sci. Prog. (Oxford)* 66:25-42.
- Hissett, R., and T. R. G. Gray. 1976. Microsites and time changes in soil microbe ecology. In The Role of Terrestrial and Aquatic Organisms in Decomposition Processes, edited by J. M. Anderson and A. Macfadyen, pp. 23-29. Oxford: Blackwell Sci. Publ.
- Lousier, J. D., and D. Parkinson. 1976. Litter decomposition in a cool temperate deciduous forest. *Can. J. Bot.* 54:419-436.
- Lousier, J. D., and D. Parkinson. 1978. Chemical element dynamics in decomposing leaf litter. *Can. J. Bot.* 56: 2795-2812.
- Mitchell, M. J. 1974. Ecology of oribatid mites in an aspen woodland soil. Ph.D. thesis, University of Calgary, Alberta, Canada.
- Nagel-de Boois, H. M., and E. Jansen. 1971. The growth of fungal mycelium in forest soil layers. *Rev. Ecol. Biol. Sol.* 8:509-520.
- Parkinson, D., S. Visser, and J. B. Whittaker. 1977. Effects of Collembolan grazing on fungal colonization of leaf litter. In Coil Organisms as Components of Ecosystems, *Ecol. Bull. (Stockholm)* 25:75-79.
- Parkinson, D., K. H. Domsch, and J. P. E. Anderson. 1978. Die entwicklung mikrobieller Biomassen un organischen Horizont eines Fichtenstandortes. *Oecol. Plant* 13:355-366.
- Parkinson, D., K. H. Domsch, and J. P. E. Anderson. Studies on the relationship of microbial biomass to primary production in three spruce forest soils. *Bakt. Centrbl.* (in press).
- Parkinson, D., S. Visser, and J. B. Whittaker. Effects of Collembolan grazing on fungal colonization of leaf litter. *Soil Biol. Biochem.* (in press).
- Soderstrom, B. 1979. Seasonal fluctuations of active fungal biomass in horizons of a podzolized pine-forest soil in central Sweden. *Soil Biol. Biochem.* 11: 149-154.
- Swift, M. J. 1973. The estimation of mycelial biomass by determination of the hexosamine content of wood tissue decayed by fungi. *Soil Biol. Biochem.* 5:321-332.
- Ulrich, B., R. Mayer, and H. Heller. 1974. Data analysis and data synthesis of forest ecosystems. *Gottinger Bodenk. Ber.* 30:1-459.
- Visser, S., and D. Parkinson. 1975. Litter respiration and fungal growth under low temperature conditions. In Biodegradation et Humification, edited by G. Kilbertus et al., pp. 88-97. Sarreguemines, France: Pierron Editeur.
- Visser, S., and J. B. Whittaker. 1977. Feeding preferences for certain litter fungi by Onychiurus subtenueis. *Oikos* 29:320-325.
- Waid, J. S., K. J. Preston, and P. J. Harris. 1973. Autoradiographic techniques to detect active microbial cells in natural habitats. In Modern Methods in Microbial Ecology, *Ecol. Bull. (Stockholm)* 17:317-322.